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Heligmosomoides johnsoni sp. nov. (Nematoda: Heligmosomatidae) from the heather vole, *Phenacomys intermedius* Merriam

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Heligmosomoides johnsoni sp. nov. is described from the cecum of the heather vole, *Phenacomys intermedius* Merriam, from the Olympic Mountains, Washington. The absence of longitudinal cuticular ridges dorsally separates *H. johnsoni* from species of *Heligmosomoides* other than *H. hudsoni* (Cameron, 1937), which occurs in varying lemmings, *Dicrostonyx* spp., and from which *H. johnsoni* is distinguished by its longer spicules, form of the dorsal ray, and other characters. Both *Phenacomys* and *Dicrostonyx* have a specialized cecum, with long villi around which the nematodes are found tightly coiled. The zoogeography of heligmosomid nematodes in *Phenacomys* is briefly discussed.

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On décrit *Heligmosomoides johnsoni* sp. nov. parasite du caecum du rongeur néarctique, *Phenacomys intermedius* Merriam, des Montagnes Olympiques de Washington. L'absence de crêtes cuticulaires sur la face dorsale sépare *H. johnsoni* des autres *Heligmosomoides* à l'exception d'*H. hudsoni* (Cameron, 1937) qui se trouve chez *Dicrostonyx* spp., et duquel *H. johnsoni* se distingue par ses spicules plus longs, par la forme différente de la côte dorsale et par d'autres caractères. *Phenacomys* et *Dicrostonyx* ont un caecum spécialisé, muni de villosités allongées, autour desquelles les nématodes s'enroulent étroitement. La zoogéographie des nématodes héligmosomes chez *Phenacomys* est discutée.

Nematodes of the genus *Heligmosomoides* Hall, 1916 are parasites of rodents, characteristically inhabiting the small intestine. Among their hosts, the two arvicoline genera, *Dicrostonyx* and *Phenacomys*, are distinguished by the presence in the cecum of numerous, long villi. *Heligmosomoides hudsoni* (Cameron, 1937), known only from varying lemmings, *Dicrostonyx* spp., occurs in the cecum, coiled tightly around the long villi. Similarly localized nematodes were found in the cecum of a heather vole, *Phenacomys intermedius* Merriam, by Dr. Murray L. Johnson, Puget Sound Museum of Natural History, University of Puget Sound, who kindly provided the material for study. These nematodes represented an undescribed species of *Heligmosomoides*.

Materials and Methods

The skinned carcass of the infected animal, with viscera *in situ*, had been preserved in alcohol. The nematodes were removed and cleared by evaporation of 70% ethanol containing 5% glycerin, after which some were stained in rose bengal in glycerin. The arrangement of the cuticular structures was determined from transverse sections of cleared nematodes. Nematodes *in situ* were dehydrated in ethanol, embedded by the paraffin method, cut at 0.010 mm, and stained in hematoxylin-eosin.

Results

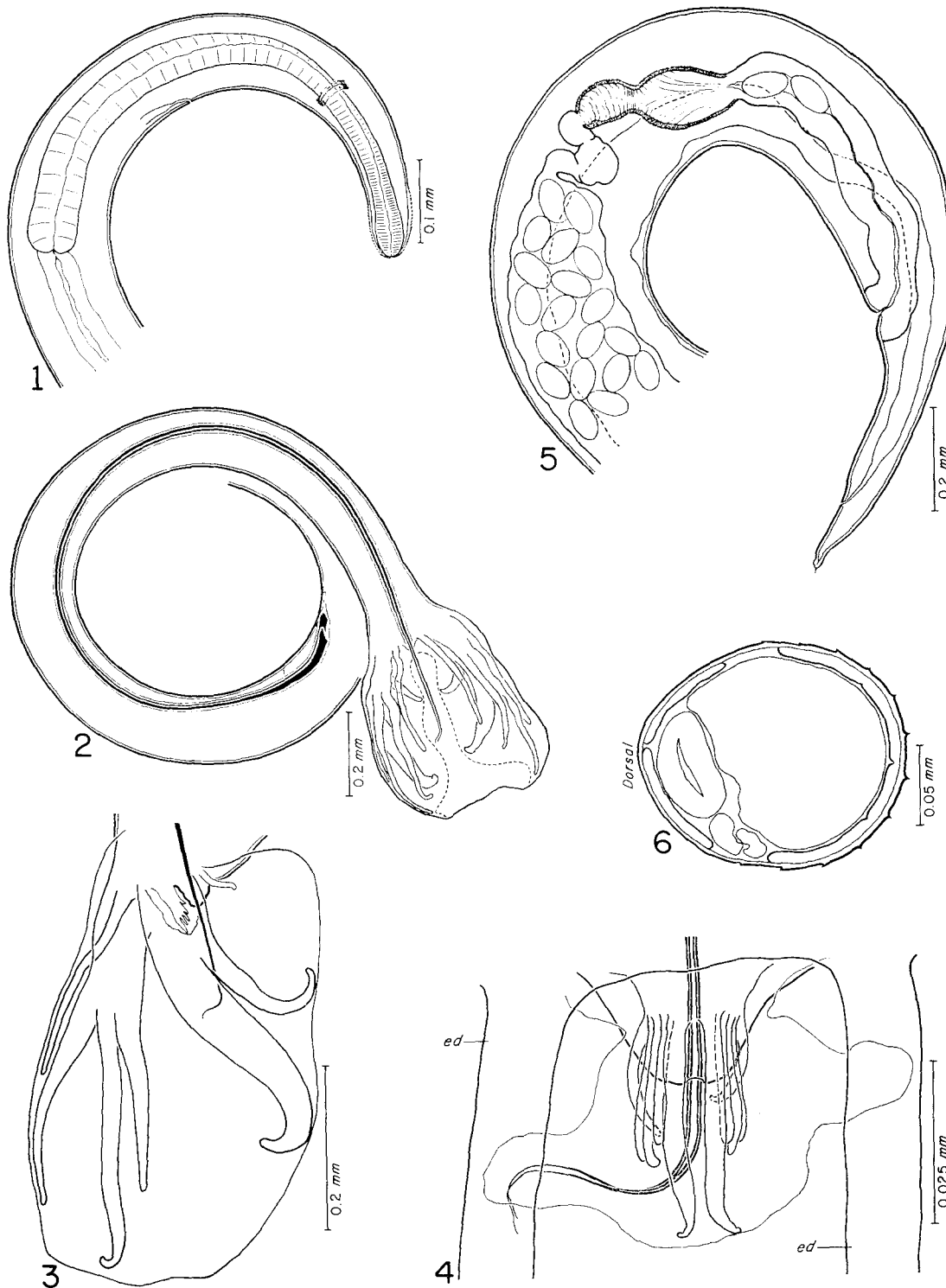
The nematodes, red when alive, were coiled sinistrally around the villi, forming six or seven

loops, and becoming partially embedded in the mucosa as the strangulated villi increased in diameter. The following description is based upon seven males and seven females. Measurements are in millimeters, with averages (av) in parentheses.

Heligmosomoides johnsoni SP. NOV.

(Figs. 1-6)

MALE: Length 6.2 to 7.1 (av 6.5). Maximum diameter, at level about three-fifths of length from anterior extremity, 0.200 to 0.235 (0.210). Width at anterior end, 0.032 to 0.040 (0.035). Width at base of oesophagus, 0.115 to 0.156 (0.130); at level just anterior to bursa, 0.114 to 0.157 (0.139). Cephalic inflation about 0.098 by 0.055. Excretory pore 0.332 to 0.405 (0.368) and nerve ring 0.194 to 0.205 (0.200) from anterior extremity. Distance from nerve ring to excretory pore 0.137 to 0.162 (0.149). Cuticle about 0.003 thick, provided ventrally with 11 or 12 longitudinal ridges, 0.0016 to 0.0032 high, and decreasing in height dorsad. Oesophagus 0.583 to 0.641 (0.613) long and 0.053 to 0.060 (0.057) wide at base. Spicules subequal, 2.21 to 2.46 (2.36) long, with attenuated, slender tips; each consisting of two cylindrical processes discernible in cross section. Bursa slightly asymmetrical, with dextral lobe larger, 0.300 to 0.560 (0.424) long by



0.259 to 0.400 (0.308). One pair of prebursal papillae, 0.032 to 0.048 long, present ventrally (see Fig. 3). Genital cone well developed. Dorsal ray complex, having five slender projections bilaterally, of which medial pair is about 0.035 long; four lateral pairs shorter, and nearly uniform in length. Slender externodorsal rays 0.154 to 0.250 (0.202) long. Common trunk of lateral rays short. Anterolateral rays 0.186 to 0.288 (0.236), mediolateral rays 0.235 to 0.389 (0.320), and posterolateral rays 0.235 to 0.356 (0.299) in length. Anteroventral rays 0.130 to 0.280 (0.215) long; thick posteroventral rays 0.211 to 0.320 (0.302) long. Bursal membrane well developed.

FEMALE: Length 8.2 to 17.7 (av 11.9). Maximum diameter, at level about three-fifths of length from anterior extremity, 0.250 to 0.286 (0.264). Width at anterior end, 0.040 to 0.055 (0.048). Width at level of nerve ring, 0.102 to 0.108 (0.105); at base of oesophagus, 0.138 to 0.214 (0.164); at level of vulva, 0.121 to 0.157 (0.137); at level of anus, 0.039 to 0.062 (0.051). Cephalic inflation 0.099 to 0.113 long by 0.065 to 0.081. Excretory pore 0.339 to 0.449 (0.387) and nerve ring 0.206 to 0.243 (0.221) from anterior extremity. Distance from nerve ring to excretory pore 0.130 to 0.206 (0.169). Cuticle provided ventrally with 12 longitudinal ridges decreasing in height dorsad. Oesophagus 0.664 to 0.714 (0.694) long, and 0.055 to 0.079 (0.065) wide at base. Anus 0.109 to 0.125 (0.119) anterior to end of tail; tail provided with caudal spine 0.008 to 0.011 long. Vulva 0.478 to 0.522 (0.506) anterior to end of tail (to base of caudal spine). Vagina 0.600 to 0.745 (0.664) long. Ovijector 0.189 to 0.305 (0.233) long, with anterior chamber averaging 0.070 by 0.057 and posterior chamber averaging 0.163 by 0.086. Thin-shelled eggs 0.079 to 0.089 by 0.040 to 0.057 (0.082 by 0.046).

TYPE HOST: Heather vole, *Phenacomys intermedius* Merriam.

TYPE LOCALITY: Hurricane Ridge, Mt. Angelus Trail, Olympic Peninsula, Clallam County, Washington, U.S.A.

HABITAT: Cecum of host.

TYPES: U.S. National Museum Helmintho-

logical Collection No. 72664 holotype (male) and allotype; No. 72665 paratype. Paratypes also deposited at Puget Sound Museum of Natural History.

Comparisons

The genus *Heligmosomoides* includes 24 species, of which 10 have been recorded in North America (Durette-Desset 1971; Durette-Desset *et al.* 1972). Two species, *H. hudsoni* (Cameron, 1937) and *H. polygyrus* (Dujardin, 1845), the latter represented in North America by two subspecies, are holarctic in distribution. *H. johnsoni* sp. nov. is probably host specific for *Phenacomys*, a nearctic genus of rodents, in which it is adapted to conditions provided by the specialized cecum. Consequently, it is compared only with species of *Heligmosomoides* known from North America.

Eight nearctic species and a subspecies of *H. polygyrus* occur in arvicoline rodents: *bullosus* Durette-Desset, 1967 (with two subspecies); *carolinensis* (Dikmans, 1940); *hudsoni* (Cameron, 1937); *longispiculatus* (Dikmans, 1940); *microti* (Kuns and Rausch, 1950); *montanus* Durette-Desset, 1967; *tenorai* Durette-Desset, 1967; *wisconsinensis* Durette-Desset, 1967; and *polygyrus americanus* Durette-Desset, Kinsella, and Forrester, 1972. *H. douglasi* Durette-Desset *et al.*, 1972 is known only from a cricetid, and *H. polygyrus bakeri* Durette-Desset *et al.*, 1972 occurs in murids and cricetids.

Direct comparisons were made with *H. hudsoni*, from a varying lemming collected by one of us at Point Barrow, Alaska, and with *H. polygyrus americanus*, obtained from a heather vole by Dr. M. L. Johnson. The infected animal was born in captivity from a pregnant female captured in Linn County, Oregon, by Mr. Chris Maser, Puget Sound Museum of Natural History. *H. johnsoni* resembles *H. hudsoni* in lacking cuticular ridges dorsally, in having bursal rays of similar relative lengths, and in the female, in having the vulva situated relatively far anterior to the anus. The male *H. johnsoni* is a smaller nematode, but the spicules are much longer than are those of *H. hudsoni* (1.4–1.5 mm). It differs

FIGS. 1–6. *Heligmosomoides johnsoni* sp. nov. Fig. 1. Anterior end of female. Fig. 2. Caudal end of male, dorsal view. Fig. 3. Bursa of male, lateral view. Fig. 4. Genital cone and dorsal ray of male, dorsal view; *ed* = externodorsal ray. Fig. 5. Caudal end of female, lateral view. Fig. 6. Transverse section of female, two-thirds of distance from anterior end, showing arrangement of cuticular ridges.

from *H. hudsoni* also in form of dorsal ray, in having a relatively longer oesophagus, and in the female, in size of egg (0.070 by 0.050 in *H. hudsoni*). *H. johnsoni* differs from *H. p. americanus* in number and disposition of cuticular ridges, in having much longer spicules (0.87 to 0.95 in *H. p. americanus*), in form of dorsal ray, and in the female, in the more anterior position of the vulva.

The absence of cuticular ridges dorsally separates *H. johnsoni* from the remaining species; the dorsal ray of *H. johnsoni* also appears to be distinctive in form. The spicules are distinctly shorter (less than 2 mm) in *bullosus*, *carolinensis*, and *douglasi*, and much longer (3.9 mm or more) in *longispiculatus* and *montanus*. The spicules of *H. johnsoni* are similar in length to those of *microti*, *tenorai*, and *wisconsinensis*; it differs from these in having relatively short externo-dorsal rays, and in proportions of other structures. The female *H. johnsoni* is further distinguished by the more anterior location of the vulva, the relative proportions of other structures, and in some cases by size of egg.

Dr. M. L. Johnson first observed that *H. johnsoni* produces distinctive lesions in the cecum of the host, as does *H. hudsoni* in *Dicrostonyx*. These lesions will be described elsewhere.

Discussion

Heligmosomoides hudsoni and *H. johnsoni*, inhabiting the cecum of *Dicrostonyx* spp. and *Phenacomys intermedius*, respectively, have in common, morphological characteristics that distinguish them from the remaining species of *Heligmosomoides*. The morphological similarities are probably a result of convergent evolution in two species that have become adapted to the unique biotope provided by the specialized cecum of the hosts. *Dicrostonyx* is considered to be the most primitive of the lemmings and, on morphological grounds, one of the most isolated of the genera in Arvicolinae (Hinton 1926). Of palaearctic origin, *Dicrostonyx* appears to have become established in North America during early Rancholabrean (preWürm) time (Repenning 1967). *Phenacomys* is a nearctic genus that can be traced to the late Pliocene (Simpson 1945). The genera in Arvicolinae are considered at the present time to be polyphyletic (Repenning 1968).

Durette-Desset *et al.* (1972) have postulated a dual origin for species of *Heligmosomoides* in

North America. According to their hypothesis, most nearctic species arose after the introduction of ancestral forms as a result of faunal interchanges during Pleistocene time. A second group, consisting of the two subspecies of *H. polygyrus*, differentiated from populations in house mice, *Mus musculus* L., introduced from Europe during the period of colonization of North America. Zoogeographic evidence indicates that *H. hudsoni* entered North America with the precursor of the Recent forms of *Dicrostonyx* not later than the penultimate glacial period (early Rancholabrean time) (Rausch and Rausch 1972). *H. johnsoni* may be of comparably ancient origin, or it possibly is derived from *H. hudsoni*, having adapted to *Phenacomys* after populations of *Dicrostonyx* were displaced southward by the Würm glaciation. Remains of both *Dicrostonyx* and *Phenacomys* have been found in late Pleistocene deposits in Pennsylvania (Guilday and Douth 1961).

The origin and taxonomic status of *H. polygyrus americanus* appear to be more obscure. This nematode has been recorded in Oregon and Montana by Durette-Desset *et al.* (1972). Schad (1954) reported *Nematospiroides dubius* Baylis, 1926 (= *H. polygyrus*) from a vole, *Microtus chrotorrhinus* (Miller), from the Province of Quebec, in eastern Canada. It was subsequently determined by Peterson (1962) that the host was instead *Phenacomys ungava* Merriam (= *P. intermedius celatus* Merriam). From the study of Schad's material, Durette-Desset *et al.* (1972) concluded that the species was *H. p. americanus*. This nematode thus appears to occur in *P. intermedius* throughout its geographic range. Since it must be assumed that adaptation to *Phenacomys* would have involved a single population of *H. polygyrus*, it does not seem possible that this nematode could have attained its extensive geographic distribution within the period of time specified by Durette-Desset *et al.* (1972). The problem is complicated also in that some subspecies of *P. intermedius* have disjunct ranges in mountainous regions of western North America. The occurrence of *H. p. americanus* in such isolated populations (e.g., the Olympic Mountains of western Washington) would support the hypothesis that this nematode was a widely distributed parasite of *P. intermedius* before the range of this rodent was modified by events of the last glacial period. Further investigation may

show that *H. p. americanus* is a distinct species restricted in occurrence to *Phenacomys*.

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